THE APPARATUS COMPOSITION AND ARCHITECTURE OF *ERISMODUS QUADRIDACTYLUS* AND THE IMPLICATIONS FOR ELEMENT HOMOLOGY IN PRIONIODININ CONODONTS

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Abstract: The apparatus composition and architecture of prioniodinin conodonts is poorly understood, largely because few prioniodinin taxa are represented by articulated oral feeding apparatuses (natural assemblages) in the fossil record, but also due to the highly variable gradational morphology of their constituent elements that makes apparatus reconstruction problematic. We describe here a natural assemblage of *Erismodus quadridactylus* (Stauffer), a prioniodinin, from the Sandbian (Late Ordovician) of North Dakota, USA. The assemblage demonstrates that the apparatus architecture of *Erismodus* is similar to those of late Palaeozoic prioniodinins namely, *Kladognathus* Rexroad and *Hibbardella* Bassler, but also has similarities with ozarkodinin apparatuses. In addition, there is evidence to suggest that *E. quadridactylus* also shares topological similarities to 'prioniodontid' architecture, with respect to the position of its inferred P elements. The apparatus composition and architecture presented here indicate that, at least with respect to the M-S array, an 'ozarkodinin-type' bauplan is likely more widely representative across prioniodontids. The assemblage demonstrates that element morphotypes traditionally considered to lie within the S array are M elements, whereas others traditionally interpreted as P elements are found in the S array. These observations are used as a basis for refining concepts of element homology among prioniodinin conodonts and their closest relatives.

Key Words: Prioniodinina, Ordovician, conodont, apparatus architecture, phylogeny

CONODONTS were soft-bodied, cyclostome-like creatures, which bore a differentiated assemblage of oropharyngeal elements constituting a feeding apparatus (Sweet 1988; Aldridge *et al*. 1986, 1993). These phosphatic elements form the bulk of the conodont

fossil record, and are found in Late Cambrian through to end-Triassic sediments. Following the discovery of body fossils (Briggs *et al*. 1983; Aldridge *et al*. 1986, 1993), conodonts were confirmed as vertebrates (Aldridge *et al.* 1986; Donoghue et al. 2000). Attempts to reject a vertebrate affinity (Turner et al. 2010; Blieck et al. 2010) are unconvincing. Thus, the study of their evolution has the potential to yield valuable data on the early evolutionary history of vertebrate skeletal, nervous, locomotory and feeding systems.

Conodont body fossils remain rare and the majority of conodont research is based on the identification and analysis of discrete elements of the feeding apparatus derived from the dissolution or disaggregation of marine rocks. In some cases, these elements can be found as 'natural assemblages' where clusters of adjacent elements were fused during diagenesis, or where the apparatus of a single individual is preserved upon a single bedding plane. Assemblages such as these have enabled the construction of precise three-dimensional architectural models and an improved understanding of the function of the feeding apparatus of conodonts (Aldridge *et al*. 1987, 1995; Sansom *et al.* 1994; Purnell and Donoghue 1997, 1998; Smith *et al.* 2005; Aldridge *et al*. 2013). They also serve as the basis of a topology-based homology framework for elements (Purnell *et al.* 2000), underpinning attempts to establish a phylogenetic nomenclature in conodont systematics (Donoghue *et al.* 2008).

The *Erismodus* assemblage described here is the first natural assemblage of an Ordovician prioniodinin, facilitating the development of an architectural model. *Iowagnathus* Liu *et al.* (2017), from the Middle Ordovician of Iowa, may also be a primitive prioniodinin, with digyrate P elements and peg-like denticles, but the taxon is highly autapomorphic and the phylogenetic relationships are not known.

Few prioniodinin taxa are represented by natural assemblages, and the only others for which architectural reconstruction has been possible are *Kladognathus* Rexroad, 1958, and *Hibbardella* Bassler, 1925, both of which have fifteen element apparatuses (Purnell 1993; Nicoll 1977). *Idioprioniodus* Gunell, 1933, another derived prioniodinin for which natural assemblages have been recovered, also comprises a 15-element apparatus made up of P, M and S elements. However, details of the apparatus composition and architectural plan of this taxon are yet to be determined in detail (Purnell and von Bitter 1996).

On the basis of these assemblages, Purnell and Donoghue (1998) and Purnell *et al*. (2000) hypothesised that prioniodinin apparatuses comprised fifteen elements, with pairs of P_1, P_2, S_1-S_4, and M elements and the S_0 element as the only unpaired component. Purnell (1993) stated that detailed similarities between prioniodinin and ozarkodinin assemblages, such as the number of elements within the apparatus, the orientation of lateral or anterior processes in S elements, and the uncertainty regarding the exact position of the M elements, indicate a similar position and orientation of elements within the two groups. The new specimen of *Erismodus* affords an opportunity to compare the architecture of ozarkodinin and prioniodinin feeding apparatuses.

PHYLOGENETIC STATUS AND APPARATUS COMPOSITION OF THE PRIONIODININ CONODONTS

Taxonomically, prioniodinin conodonts are not phylogenetically well resolved within the Conodonta and this is reflected in differing opinions regarding their relationships. Sweet (1988) recognised the Prioniodinida as a monophyletic group but it was not resolved in a strict phylogenetic sense and Sweet could not identify the ancestry of *Erraticodon* Dzik, 1978, the oldest known member of his Prioniodinida. In contrast, Dzik (1991) combined the Prioniodinida (*sensu* Sweet 1988) with the Ozarkodinida, which also contained some prioniodontid (*sensu* Sweet 1988) taxa such as *Periodon* (Hadding 1913). The differences between these two influential classification schemes are partly the result of an implicit, underlying assumption that the fossil record of conodonts is complete and, therefore, a chronostratigraphically faithful phylogeny could be derived.

Subsequent revisions have been made to Sweet's classification (Aldridge and Smith 1993), and Sweet and Donoghue (2001, fig. 6) tentatively recognised the Prioniodinida as monophyletic and the sister lineage of the Ozarkodinida. The most recent cladistic analysis (Donoghue *et al*. 2008) aimed to elucidate the phylogenetic relationships between the three orders of 'complex' conodonts and exhibits similarities and differences to both the Sweet and Dzik phylogenies. Overall, it broadly confirms the framework of Sweet's scheme and comprises two major clades, the Prioniodinina and Ozarkodinina (which are approximately equivalent to Sweet's Prioniodinida and Ozarkodinida, respectively), together with a paraphyletic array of sister clades assigned by Sweet to the Prioniodontida. 'Prioniodontids' are, nevertheless, a grade of conodonts recognised by most conodont workers and have some utility within the context of this paper: non-prioniodinin, non-ozarkodinid prioniodontids are thus referred to in this paper as 'prioniodontids'.

Following Donoghue *et al.* (2008), prioniodinins and ozarkodinins comprise a clade to the exclusion of *Promissum pulchrum* Kovács-Endrödy, 1986, a derived 'prioniodontid' conodont for which the apparatus architecture is well-understood and in which the positional homologies are well-constrained owing to data derived from hundreds of assemblages (Aldridge *et al*. 1995). Thus, it is appropriate to expect that their last common ancestor at least shared the characteristics that are shared by ozarkodinin conodonts and *P. pulchrum*. These characteristics include the location, number and the orientation of M elements, which are positioned to the anterior of the S array, the presence of at least three pairs of S elements and, to some degree, the orientation and position of the S elements (with the exception of the S_0 element that lies on the rostro-caudal axis), which are inclined forwards and inwards. In addition, the S elements are located in an increasingly dorsal and anterior position away from the rostro-caudal axis (Purnell and Donoghue 1998).

The taxonomic difficulties relating to prioniodinins are also a result of poorly understood apparatus composition and architecture. Of the three orders of 'complex' or 'higher' conodonts recognised by Sweet (1988) – the Prioniodontida, Prioniodinina and

Ozarkodinina – prioniodinins are the least understood in an architectural and phylogenetic sense. Firstly, this is because the apparatuses of prioniodinin conodonts are composed of similarly shaped elements, whereas the morphologies of the P, S and M element domains of 'prioniodontid' and ozarkodinin conodonts are markedly distinct from each other, making it easier to reconstruct apparatuses and infer homologies. Secondly, hundreds of natural assemblages of ozarkodinin taxa have been discovered and studied in great detail (cf. Aldridge et al. 1987; Purnell and Donoghue 1998). These studies confirm that taxa within the Ozarkodinina had a distinctive apparatus with two pairs of P elements, a symmetrical unpaired S_0 element, four pairs of S elements (S_1 to S_4), and one pair of M elements, making a total of 15 elements within the apparatus (Aldridge *et al*. 1987). Further architectural analyses facilitated the construction of a three-dimensional model that relates element positions to each other within the apparatus of an ozarkodinin conodont. The most distinctive feature of this apparatus pattern is that the S element array lay with an angular relationship to the P elements, which in turn had their long axes ('anterior–posterior') approximately parallel to the dorso-ventral axis. 'Prioniodontid' conodonts are also well represented by natural assemblages, particularly by *Promissum pulchrum* – a 'prioniodontid' that may be unusual in having two additional pairs of P elements (P_3 and P_4; Aldridge *et al*. 1995). Additional P elements were also recorded by Aldridge *et al.* (2013) in *Notiodella keblon*, another prioniodontid from the Soom Shale of South Africa, which has a pair of P_3 elements in addition to the P_1 and P_2 pairs.

In contrast to the availability of ozarkodinin and 'prioniodontid' assemblages, only a few prioniodinin taxa are represented by bedding plane assemblages (Rhodes 1954; Purnell 1993; Purnell *et al*. 2000; Nicoll 1977) together with a few fused clusters, most of which are incomplete and yet to be interpreted architecturally (e.g. Lange 1968; Ramovš 1977, 1978; Mietto 1982; Igo *et al.* 1988). There is one complete assemblage of *Hibbardella angulata* (Nicoll 1977) described to date, together with some assemblages of *Idioprioniodus* (Schmidt and Müller 1964; Purnell and von Bitter 1996) and an assemblage of *Kladognathus* (Purnell 1993). With respect to current phylogenetic schemes (Sweet 1988; Dzik 1991; Donoghue *et al*. 2008) these assemblages represent relatively derived taxa within the clade and their apparatus architectures conform with those of the Ozarkodinina; it has therefore been predicted that basal prioniodinin conodonts possessed a similar default 15 element architectural 'blueprint' (Purnell 1993; Purnell *et al*. 2000).

HOMOLOGY

The earliest reconstructions of isolated elements into multielement apparatuses, relied heavily upon the theory of 'symmetry transition series' whereby the recognition of progressive symmetry between S elements was believed to identify their position within the apparatus, with elements becoming more asymmetrical away from the symmetrical axial element of the S array (Lindström 1964; Bergström and Sweet 1966; Walliser 1964; Sweet and Schönlaub, 1975; Sweet 1981, 1988). However, work on ozarkodinin

apparatuses has shown that although this is a useful approach when recognising and grouping elements from discrete collections, it has no value when discerning positional homologies (Purnell and Donoghue 1998; Purnell *et al*. 2000). The natural assemblage of *Erismodus quadridactylus* (Stauffer 1935) possesses complete *in situ* elements making up the apparatus of a phylogenetically primitive Ordovician prioniodinin. The assemblage provides a template from which element homologies of closely related taxa can be extrapolated and thus the complexity of the prioniodinin apparatus can be better constrained and understood.

MATERIALS AND METHODS

The bedding plane assemblage of *Erismodus quadridactylus* (USNM 542388) is from Sandbian (Late Ordovician) strata in the Shell Oil Duerre 43-5 well, which was drilled in section 5, Township 163 North, Range 87 West, in Renville County, North Dakota, USA. The well is in the Newporte Field of the Williston basin.

The assemblage was imaged at the Natural History Museum, London, using an ISI ABT-55 Environmental SEM with large specimen chamber at low vacuum and 20 kv (Figs 1A, 2A). Following preparation to remove a loose flake on the part in order to investigate the possible presence of additional elements, a second set of images was taken at the Natural History Museum using a LEO 1455 variable pressure SEM in back-scatter mode (Figs 1B, 2B). A composite line drawing of the part and counterpart (Fig. 3) was produced by tracing the SEM images; minor adjustment was necessary to compensate for minor distortion in the SEM images. The remaining specimen (i.e. without the isolated flake) was CT scanned using a Nikon Metrology XTH225ST at the School of Earth Sciences, University of Bristol; the flake was scanned separately using the TOMCAT X02DA beamline at the Swiss Light Source, Paul Scherrer Institute, Villigen, Switzerland. The sample was scanned mounted in a 2 µl pipette tip packed with powdered sugar. We used a 4x objective, LuAg:Ce 20 µm scintillator, 18 keV energy and an exposure time of 130 ms, acquiring 1501 projections equiangularly over 180°. Projections were post-processed and rearranged into flat- and dark-field-corrected sinograms. Reconstruction was performed on a 60-core Linux PC farm using a Fourier transform routine and a regridding procedure (Marone *et al.* 2010). The resulting volume has isotropic voxel dimensions of 1.625 µm. Slice data were analysed and manipulated using the computed tomography software SPIERS version 2.2 (Figs 4, 5). The specimen is deposited in the National Museum of Natural History, Washington DC, USA, and the tomographic data and reconstructions are available (Dhanda *et al.* 2018)

TAXONOMIC IDENTITY OF THE ASSEMBLAGE

The Prioniodinida *sensu* Sweet (1988) consist of at least 45 genera, most of which are made up of rather isomorphous element morphotypes within the apparatus of a single species. The Chirognathidae *sensu* Sweet (1988) comprise taxa with elements that are broadly similar to those in the assemblage, with the Ordovician taxa *Erraticodon* Dzik, 1978, *Chirognathus* Branson and Mehl, 1933, and *Erismodus* Branson and Mehl, 1933

– all bear elements that possess tall robust cusps, elongate denticles and are intergradationally variant. *Erraticodon* is distinguished by processes upon which the denticles vary in size dramatically, and v-shaped spaces between the denticles that are fused within the bar. The elements in the assemblage have U-shaped spaces between their denticles and do not exhibit large variations in denticle height upon the same process, so any direct attribution to *Erraticodon* is considered unlikely.

Chirognathus has denticles that are curved in a 'posterior' direction along with the processes. The pattern of denticulation is similar to that of *Erraticodon* where the denticles vary in size upon the same process and have v-shaped spaces between them, so it not likely that the assemblage belongs to this genus either. The Family Chirognathidae also includes the genus *Erismodus* that comprises five known species. This genus was defined by Sweet (1988) as having a septimembrate apparatus where the elements bear discrete peg-like denticles that taper to a point. Denticles vary in size upon the same process but not as dramatically as seen in *Erraticodon*. Some species of *Erismodus* tend to have an anticusp or 'distally rounded boss' (*sensu* Branson and Mehl 1933) but as this is quite variable between species it is not considered a definitive generic feature because it mostly defines the morphology of the type species, which displays the most pronounced 'boss' (Sweet 1988). The assemblage is thus considered to be a species of *Erismodus*.

The multielement apparatus of Erismodus

Initial attempts to deduce the multielement apparatus composition of species of *Erismodus* were made by Andrews (1967) who noted that his collections of *Erismodus* from the Joachim Dolomite, Missouri, 'exhibited a wide range of variability generically with few characteristics suitable for speciation other than by placing symmetrically identical elements together'. Andrews formulated an elaborate hypothesis in which he proposed that individual species of *Erismodus* display increased element asymmetry with time. Four species were documented, of which the oldest was the relatively symmetrical *Erismodus typus*, succeeded in turn by *Erismodus symmetricus*, *Erismodus asymmetricu*s, and *Erismodus gracilis*. These species have since been subsumed into subsequently erected multielement reconstructions of *Erismodus* (Sweet 1982; Bauer 1990, 1994; Fig. 6).

Subsequently, Votaw (1971) observed 'transitional symmetry' between respective elements of an apparatus. However, he did not observe a trend towards asymmetry with time. Votaw used ratios of the frequency of 'like' elements to determine the apparatus of *Erismodus radicans* (Hinde 1879) and concluded that it comprised five individual element types: microcoelodiform, erismodiform, ptiloconiform, dichognathiform and eoligonodiniform. Carnes (1975) also separated his collections into morphotypes using the angle observed between the two lateral processes of an element when viewing the element apically. His results yielded two distinct apparatuses, each consisting of seven element types that he labelled using form taxonomic terminology: symmetrical trichonodelliform, asymmetrical

trichonodelliform, zygognathiform, eoligonodiniform, prioniodiniform and 'modified falodontiform' elements. *Erismodus* sp. 2 was distinguished on the basis of its longer and more compressed denticles in comparison with *Erismodus* sp. 1. Subsequently, a number of reconstructions of species of *Erismodus* were proposed in unpublished Masters and PhD theses (Boger 1976; Schmidt 1982; Hall 1986; Fig. 6). However, due to a badly preserved type specimen, a limited generic description and the lack of a comprehensive species concept for *Erismodus*, many authors have expressed difficulties in assigning specific names consistently to reconstructed apparatuses and have therefore resorted to open nomenclature (e.g. Smith 1985; Rexroad *et al.* 1982; Ethington *et al*. 1986; Copeland *et al*. 1989; Leslie 2001; Zhang *et al*. 2003; Witzke and Metzger 2005). Although attempts at reconstructing individual species have been made (Sweet 1982; Zhang *et al*. 2003), Leslie (2001) stressed that in order to understand species of this genus fully and to differentiate their apparatuses with confidence, there was a need for an extensive restudy of all type specimens, the bulk samples from which they were described, and the definition of an apparatus concept for the type species.

An additional problem of working with *Erismodus* and other prioniodinin conodonts includes the common but variable presence of distorted and twisted elements. Ethington *et al*. (1986), for example, observed that their collection of elements had 'strong salients in the aboral margin', a feature not common in specimens found from the Harding Sandstone or the Joachim Dolomite. They suggested that these differences were perhaps the result of environmental influences. The influence of environmental factors on conodont growth is a topic that is not well understood and it is possible that some conodont species are likely to have been misinterpreted on this basis. A detailed study of a variety of samples across a number of stratigraphic localities may yield insights into this subject, but this is beyond the scope of the current study.

Species identity of the assemblage

The genus *Erismodus* comprises five multielement species: the type species *E. typus* (Branson and Mehl 1933), *E. radicans* (Hinde 1879), *E. quadridactylus* (Stauffer 1935), *E. arbucklensis* Bauer, 1987, and *E. nicolli* Zhang, Barnes and Cooper, 2003. The genus is defined by a septimembrate apparatus with elements that bear discrete peg-like denticles, which taper to a point. The denticles also vary in size upon the same process but not as dramatically as seen in taxa such as *Erraticodon*. Some species have an anticusp or 'distally rounded boss' developed (*sensu* Branson and Mehl 1933). This pronounced anticusp, as seen in *E. typus*, is not a feature of the natural assemblage and this species can be excluded from consideration.

Erismodus arbucklensis is distinguished from other species of *Erismodus* by having an S_0 element with a cusp that is markedly compressed laterally and S elements that have widely spaced, marginally costate denticles, which are compressed 'antero-posteriorly'. The element denticles of the assemblage are sub-rounded and although the denticles are discrete they are not as widely spaced as those of *E. arbucklensis*. The elements of *E. arbucklensis* also have a relatively high bar with respect to congeneric

species, and from the assemblage it is visible that the bar is not as high. As noted above, the bar was not mineralised beyond the first three denticles on any process, but even beneath those first three denticles the bar is particularly thin. On this basis, *E. arbucklensis* does not compare closely with the natural assemblage.

Erismodus radicans is characterised by a long, robust cusp and relatively short, discrete peg-like denticles, which is clear in material figured by Hinde (1879), Carnes (1975) and Leslie (2001). This material also shows the presence of conspicuous costae on the lateral margins of the cusps. The elements of *E. radicans* are very similar to those of the assemblage, but the denticles are much shorter and therefore it is not considered to be represented by the assemblage.

Erismodus quadridactylus was first species to be fully reconstructed in the multielement sense, by Sweet (1982), who also revised the generic diagnosis. *Erismodus quadridactylus* is characterised by a long, robust cusp and relatively long, laterally compressed denticles. The latter are discrete and taper to sharp points. The most recently erected species of the genus is *Erismodus nicolli*, which although being generally similar to *E. quadridactylus* has a lesser cusp to denticle height ratio, with denticles that are approximately one-sixth the height of the cusp or less.

Of all the species of *Erismodus*, it is the elements of *Erismodus quadridactylus* that match most closely those of the natural assemblage and this assignment to species can be made with some confidence.

DESCRIPTION OF NATURAL ASSEMBLAGE

The natural assemblage is composed of a number of distinct elements plus disassociated denticles, some of which appear to be unfused discrete denticles of otherwise fused elements; other denticles are less clearly associated. The majority of the elements are exposed on the surface of the part, counterpart, and the separate flake. The following description is based on a composite camera lucida drawing (Fig. 3) that integrates all of these components. The extent of some elements and denticles has only been revealed through X-ray tomography (Fig. 4).

Complete elements

Eleven complete elements are distinguishable in the assemblage, and the numbered elements are used as the basis for description to avoid *a priori* assumptions of homology (Fig. 3). All elements are ramiform and bear long, slender, laterally compressed, keeled but acostate denticles with a biconvex cross-sectional profile. Most denticles are sub-parallel to each other but the distal denticles of processes are discrete, rather than fused as a continuous process. The fused parts of the processes of all elements are short and it is noteworthy that the elements would look significantly different if preserved in isolated collections; this may explain some of the difficulty experienced with basal prioniodinin taxonomy and apparatus reconstruction. The assemblage consists of five extensiform digyrate elements, two breviform digyrate elements, three bipennate elements, and one alate element. The maximum length of the

bedding plane assemblage (parallel to the inferred rostro-caudal axis, see below) is 4.06 mm; maximum width (perpendicular to the inferred rostro-caudal axis) is 2.86 mm. In the following descriptions, in order to avoid confusion between descriptive and interpretative terms, note that all orientations refer to traditional isolated element conventions *sensu* Sweet (1981) rather than the *in vivo* notation of Purnell *et al*. (2000).

Element 1. Bipennate. Cusp erect, slender, biconvex cross-section, laterally compressed with faint costa upon central part of the inner lateral face of distal end of cusp that swells proximally into a carina, leading into the inner lateral process; a shallow sulcus lies to the posterior of carina; posterior process has seven denticles preserved although fourth denticle is mouldic. All compressed in the plane of the process length, with distinct keels; first three basally fused, erect and parallel to cusp; remaining four discrete but aligned, extending perpendicular to posterior process. First denticle slender, needle-like, a little over 1/2 of cusp height. Second and third denticles broader in lateral profile, denticle two is 3/4 cusp height and denticle three is approximately the same height as the cusp. Denticles four to seven slightly broader in lateral profile than denticle three, all approximately same height as cusp. Denticles four and five erect. Denticle five parallel to denticle four. Denticle six tilted slightly posteriorly from denticle five. Denticle seven almost parallel to denticle six and displaced 1/5 of its height relative to the other denticles of the process. Anterior process basally continuous with lateral costa, strongly deflected posteriorly and downwards forming a 135° angle with the long axis of the cusp. Basal surface of process exposed, a shallow, narrow, slit-shaped basal cavity runs along underside of processes; no pits preserved that could correspond to the base of denticles upon the process, although no denticles are preserved on or below the surface, their absence may be taphonomic. Basal cavity wide and deep beneath cusp. Maximum preserved element length is 1.48 mm; maximum height is 0.79 mm.

Element 2. Bipennate; forms pair with Element 1. Cusp erect, slender, biconvex cross-section laterally compressed with faint costa upon central part of the inner lateral face of distal end of cusp that swells proximally into a carina, leading into the inner lateral process; a shallow sulcus lies to posterior of carina. Posterior process has nine compressed, keeled denticles preserved; first four sub-parallel to cusp but with reclination increasing from one to four; the fourth is gently curved in lateral profile; denticles five to nine are aligned and also display increasing reclination, although they are displaced. First denticle slender, needle-like, a little over 1/2 cusp height. Remaining three denticles broader in lateral profile particularly at base and taper to a point, denticle two is 3/4 cusp height, denticles three and four exceed cusp height. Bases of first three denticles fused to form continuous process; junction of denticles three and four not visible but four is aligned with other denticles. Denticles five to seven are approximately of the same height as denticle four but are discrete, with unjoined bases. Denticles eight and nine evident by bases, which are joined by a continuous margin

(basal lip of the process) and aligned with denticle seven. Antero-lateral process is strongly deflected posteriorly and downwards from cusp forming a 45° angle with the anterior axis of the cusp; basal cavity narrow and slit-shaped, no pits preserved. Four short denticles are buried below the surface of the specimen, but can be distinguished in the CT data. Basal cavity wide and deep beneath cusp. Maximum preserved element length is 1.25 mm; maximum height is 0.77 mm.

Element 3. Alate. Slender cusp with prominent lateral costa; curved posteriorly from halfway up the cusp to the tip. Posterior part of base is 1/3 wider than anterior. No associated denticles. Maximum preserved element length is 0.11 mm; maximum height is 0.57 mm.

Element 4. Bipennate. Cusp slender and curved posteriorly from the base; biconvex cross-section with moderate lateral compression; base of cusp is flared; basal cavity wide and deep. Anterior process present, forming an angle of 180° with the long axis of the cusp; process is not visibly joined to the base of cusp but lies in very close proximity. Process bears four denticles; all parallel to each other, curved posteriorly and decrease in size distally. First denticle is 3/4 cusp height; fourth denticle is 1/2 cusp height. A shallow basal groove runs beneath the process. Maximum preserved element length is 0.90 mm; maximum height is 0.45 mm.

Element 5. Extensiform digyrate. Cusp, slender, erect to gently reclined, stout at base; biconvex cross-section with moderate lateral compression; posterior surface of the cusp is steeply curved and protrudes outwards, forming the posterior margin of a wide and shallowly excavated basal cavity which continues beneath processes. Two lateral processes, one short, one long. Shorter process bears five denticles, all erect and sub-parallel to the cusp; denticles slender, needle-like and decrease in height distally. First denticle is a little over 1/2 of cusp height; second denticle is a little under 1/2 of cusp height; third denticle is slightly shorter than second, the remaining two are incomplete and entirely buried in the matrix. Longer lateral process bears eight denticles, all fused basally to form a continuous process and gently curved to posterior. Denticles one to three are sub-parallel to the cusp, slender, needle-like, and increase steadily in height; denticle three is 3/4 cusp height. Remaining denticles are more robust. Fourth denticle is tallest, approximately the same height as cusp. Denticles five to eight are laterally broader at base, parallel to each other and decrease in size distally. Maximum preserved element length is 0.53 mm; maximum height is 0.45 mm.

Element 6. Extensiform digyrate. Cusp slender, curved posteriorly, biconvex cross-section with moderate antero-posterior compression. One lateral process present with three denticles preserved; denticles almost as broad as cusp at the base; tips missing;

decrease in size distally; first denticle approximately 3/4 cusp height. Beyond third denticle, mouldic impressions indicate presence of two additional denticles on this process. Maximum preserved element length is 0.45 mm; maximum height is 0.29 mm.

Element 7. Breviform digyrate. Cusp erect to gently reclined, slender, biconvex cross-section with moderate lateral compression. Two lateral processes present; one short, one long. Short lateral process forms 180° angle with long axis of cusp; bears five denticles, all of which are aligned although not fused at bases due to disruption during collapse of apparatus. Denticles are recurved posteriorly, needle-like, and decrease in size distally. First denticle is just over 3/4 cusp height; second denticle is 3/4 cusp height and gently curved; third denticle just under 1/2 cusp height; for fourth and fifth denticles only bases are visible, they are fused to each other and also to denticle three as is evident by the continuous basal lip of process. Long lateral process bears eleven denticles all fused basally; there are small gaps between denticles 4/5, 5/6, 7/8, 8/9, 10/11, although they do not disrupt the continuity of the process. The denticles form a continuous process that curves gently to the posterior. Denticles one to four are sub-parallel to the cusp; first denticle is slender, needle-like, just over 1/2 cusp height; denticles two to four are broader than denticle one and approximately 3/4 cusp height; denticles five and six are parallel to each other, slightly displaced with respect to other denticles in process, 3/4 cusp height, broad as denticles two to four; denticles seven to eleven are parallel to denticle six, gradually decreasing in size and girth distally; denticle eleven is 1/3 cusp height. Maximum preserved element length is 1.36 mm; maximum height is 0.68 mm.

Element 8. Extensiform digyrate; Overlain by Elements 9 and 10, at the surface this element consists of five preserved denticles aligned in a row. The base of the cusp, and a short process with two larger denticles are preserved below surface of assemblage. Detailed morphology of the cusp is not preserved. On the longer process denticles decrease in size gradually from the left to the right of the process. Smallest denticle is 1/4 the size of the largest. Denticles are parallel to each other and curve in a posterior direction. The shorter process is displaced relative to the longer process, but curves downwards and would form an obtuse angle with the cusp; it has two antero-posteriorly compressed denticles preserved, neither fused basally; both are broad and approx; Maximum preserved element length is 1.20 mm; maximum height is 0.42 mm.

Element 9. Extensiform digyrate; overlain by Element 10 causing fracturing and making it difficult to distinguish between denticles of the two elements. Cusp slender, gently reclined. Two lateral processes present; one short, one long. Short process curves downwards forming an obtuse angle with the cusp; has three antero-posteriorly compressed denticles preserved, none fused basally; first and second denticles as broad as cusp and of similar height; third denticle broad at base and just over 1/2 cusp height. Long process has six parallel, antero-posteriorly compressed and laterally costate denticles present; denticles decrease in height distally; first denticle is cusp height,

broad at the base, slender and basally fused to denticle two; second denticle is slender, and cusp height; denticle three is 3/4 cusp height; denticle four is 1/2 cusp height; denticle five is 1/4 cusp height. Maximum preserved element length is 1.18 mm; maximum height is 0.43 mm.

Element 10. Extensiform digyrate. Overlies Element 9 directly hence distorted. Cusp slender, gently reclined, biconvex cross- section with moderate lateral compression. Two lateral processes present, both bear antero-posteriorly compressed, marginally costate denticles; one short, one long. Short lateral process is heavily disarticulated but a couple of denticles are discernable; denticles broad and approximately cusp height; first denticle fused to cusp basally. Longer process curves downwards to form obtuse angle with cusp, bears eleven denticles; denticles one and two are sub-parallel to the cusp, slender, needle-like with broad bases which are fused to each other and the cusp; denticles three to seven sub-parallel to denticle two, broad as cusp, bases are aligned to form continuous process but not fused together; denticles eight to eleven parallel to denticle seven, decrease in girth and height distally. Maximum preserved element length is 1.45 mm; maximum height is 0.45 mm.

Element 11. Breviform digyrate. Cusp erect to gently reclined, slender, biconvex cross-section with moderate antero-posterior compression. Two lateral processes present; one short, one long. Short lateral process bears three poorly preserved denticles, only tips and associated mouldic impressions present; estimated denticle height between 1/4 to 1/2 cusp height; junction with cusp is not clearly visible. Long lateral process has eleven denticles all sub-parallel to the cusp, gently curved posteriorly and downwards; bases of denticles one to six and seven to eleven fused. Denticle one slender, needle-like with tip missing; denticles two to eight broader than one, approximately 3/4 cusp height getting shorter gradually towards distal end; denticles nine to eleven as broad as other denticles at the base, tips narrower, decrease in height distally, denticle eleven is 1/3 cusp height. Maximum preserved element length is 1.50 mm; maximum height is 0.79 mm.

Unassigned denticles

Group a. A row of six curved denticles are present in close proximity to Elements 2 and 4. The denticles themselves are fairly short and more recurved than any other set of denticles present in the assemblage; they are all of roughly the same size and girth and their bases lie sub-parallel to the posterior process of Element 2. A cusp is not distinguishable.

Group b. Two denticles that have fallen laterally and are almost superimposed. The denticles are next to the lateral process of Element 4 and are of similar size to denticle four of this process. The denticles bear lateral costae.

Group c. Two unassigned denticles with consistent orientation to those of Element 6; slender with flared basal cavities. Left denticle lies on its lateral side exposing a lateral costae and its thin profile. Denticle to the right lies with posterior face embedded in sediment.

Group d. Group of three denticles, two of which aligned in same orientation as Group c, and central one curved in opposite direction; wide basal bodies, slender. First and third denticles of similar size; the close proximity and alignment of all bases indicates they were once fused.

Group e. A couple of small curved denticles situated left of the cusp of Element 11. The denticles are in alignment with displaced denticles of Element 1; however they are curved in the opposite direction.

APPARATUS COLLAPSE AND COMPOSITION

The assemblage of *Erismodus* can be confidently interpreted as the collapsed feeding apparatus of an individual, rather than a coprolite or faecal assemblage. The latter contain fragmented elements, include elements from disparate taxa, exhibit structureless arrangements of elements and/or contain elements that are compressed together tightly. In contrast, the *Erismodus* assemblage is composed only of elements that, in discretecollections, would be attributed to this genus. Furthermore, the elements are organized into dextral and sinistral groupings and preserve aspects of the original angular relationships between the different domains of the apparatus. Although a single assemblage has limitations in terms of the extent of interpretation that can be applied, there are nevertheless many observations that can be drawn from this assemblage of *Erismodus quadridactylus* that help to constrain both apparatus composition and architecture. The architectural interpretation also provides a testable template from which positional homologies can be better constrained within closely related but more poorly known prioniodinin conodonts (for example, other species of *Erismodus*, *Chirognathus* and *Curtognathus*).

The assemblage of *Erismodus quadridactylus* exhibits a complex pattern of collapse and the level of interpretation is limited by the availability of only one assemblage. Furthermore, the components of the apparatus are morphologically similar and closely spaced, which makes it difficult to distinguish separate P, M and S element morphologies. In contrast, in most known ozarkodinin and ‘prioniodontid’ apparatuses the P, S and M elements are morphologically distinct from each other and in most cases, the P domain is disjunct from the S–M array.

Pattern and orientation of assemblage

The line of bilateral symmetry is the most striking feature of the assemblage of *Erismodus quadridactylus*. This line bisects the ramiform elements in the apparatus that are shaded in mid-grey and dark-grey on Fig. 3. The cusps of seven of the eleven

complete elements in the assemblage are inclined towards the midline and oriented with their long lateral processes sub-parallel both to each other and to the midline of the assemblage.

The rostral and caudal ends of the apparatus can be distinguished by comparison with assemblages of *Promissum pulchrum* Kovács-Endrödy, 1986, and ozarkodinin conodonts, from which it is known that the cusps are positioned at the rostral end of the apparatus and the long processes of S and M elements extend caudally (Aldridge *et al*. 1987, 1995; Purnell *et al*. 2000). Thus, the midline of the assemblage forms the rostro-caudal axis of the apparatus, splitting the assemblage into two lateral halves, one of which is more clearly preserved than the other.

The sinistral and dextral polarity (Fig. 3) may be determined by the orientation of the inner lateral processes of S elements, which are invariably abaxial in the bipennate S elements of ozarkodinin and 'prioniodontid' apparatuses (Purnell *et al*. 2000; Theron *et al*. 1990; Barrett 2000), and the digyrate S elements of prioniodinins.

Element homology

Natural assemblage data with associated soft tissues (Briggs *et al*. 1983; Aldridge *et al*. 1986, 1993, 1995; Purnell and Donoghue 1997, 1998) have revolutionised the reconstruction of conodont apparatus architecture, enabling the position and orientation of individual elements within the feeding apparatus to be precisely constrained. This knowledge has then been applied to discrete collections of elements to reconstruct multielement apparatuses by using the architectural interpretations as a template from which to work. The orientation of elements is expressed below using both the terminology of Purnell *et al.* (2000) and conventional isolated element terminology (Sweet 1981); the latter terms are placed in inverted commas for clarity.

Only two other natural assemblages of prioniodinin taxa have been described to date: *Kladognathus* Rexroad, 1958, a relatively derived Carboniferous conodont (Purnell 1993) and *Hibbardella angulata* Hinde, 1879, which compares closely in terms of apparatus architecture (Nicoll 1977) with *Kladognathus*. No soft tissues are preserved with these natural assemblages, so it is not possible to infer the precise *in vivo* orientation. However, as their three-dimensional architecture is similar to that of ozarkodinins (Purnell and von Bitter 1996; Purnell *et al*. 2000), it is also appropriate to compare the natural assemblage of *Erismodus* with the apparatus of ozarkodinins and with that of *Promissum*, for which unequivocal evidence of spatial relationships with soft tissues is known (Briggs *et al*. 1983; Aldridge *et al*. 1986, 1993, 1995; Purnell and Donoghue 1997, 1998).

Elements 1 and 2 of the *Erismodus* assemblage, constitute a pair of bipennate elements that is isolated from the other components of the assemblage. Their position in opposition to each other allow us to establish the midline of the apparatus (Fig. 3). Element 1 presents the abaxial, 'outer' face on the part (Fig. 1), and the shorter process is directed adaxially, corresponding to an 'inner lateral' position in conventional terminology. The position apart from the other elements is thus consistent with Element

1 being an M element; Element 2 is its morphologically equivalent symmetry-pair. We interpret Element 1 and 2 as sinistral and dextral, respectively, because they possess inner lateral processes that are oriented adaxially in M elements of other conodont taxa, and reconstruct them as lying at the rostral end of the apparatus, on either side of the midline. However, in previous reconstructions based on isolated element collections these elements of *Erismodus* have been interpreted as the traditional Sc components of the apparatus (Sweet 1982; Fig. 6).

Five elements (7, 8, 9, 10 and 11) situated immediately caudal to the M elements, are morphologically similar to each other, with sub-parallel long axes, and similarly oriented. The number, orientation, sequential layering and similar morphology of the elements suggest that they are part of the S array of the apparatus. In concordance with ozarkodinin apparatuses and that of *Promissum pulchrum*, the individual S elements are oriented with their cusps at the rostral end of the apparatus and their long posterior processes extending caudally. It follows that the M elements are thus positioned rostrad of the S elements. The S elements lie with their long axes sub-parallel to the rostro-caudal axis of the conodont, but a single assemblage makes it impossible to determine from collapse pattern the exact angles with regards to the dorso-ventral or sinistral-dextral orientations of the S array within the apparatus.

In the sinistral and better-preserved half of the assemblage, the S elements in order of sequence from the midline are elements 8 to 11. In each of these elements the denticles decrease in size caudally, and the cusp lies at the rostral end of the process. They each have short adaxial processes oriented similarly to the M^s element, indicating that they form the sinistral half of the ramiform array. In the part they overlap adaxially from 11 to 8, reflecting positional homologues S_4^s-$S1^s$. S_1^s and S_2^s are approximately (but not completely) parallel and have a high angular relationships to the long processes of S_3^s (approximately 40˚) and S_4^s (approximately 25˚) elements.

Element 7 is the symmetry pair of either Element 10 or 11, which are morphologically similar. Therefore, we cannot discriminate between an interpretation as a dextral S_3 or S_4, but the element is most comparable in morphology to element 11 (S_4). In reconstructions based on isolated element collections, the S_4 digyrate elements (Element 11) were described as Sba elements by Sweet (1982); the S_3 digyrate elements were described as zygognathiform elements by Carnes (1975) and Hall (1986), and as the Sbb element in the reconstruction of of *Erismodus quadridactylus* by Sweet (1982). The symmetry pairs of Elements 8 and 9 (S_1^s, S_2^s respectively) are not preserved intact, but may be represented by the denticles in group d. In previous discrete element reconstructions (Sweet 1982, 1988) these elements have been interpreted as P_1 elements.

Element 3 is a single, tall, robust, uncurved, cusp, which has only one lateral costa visible but a symmetrical cusp cross-section. The cusp lies rostrad to the described S elements but slightly caudad to the M elements. The element is incomplete with no associated lateral processes visible, and although it is slightly displaced, and now fragmentary, it is the most likely candidate for the S_0 element (Fig. 6).

Elements 5 and 6 are set apart 'stratigraphically' from the rest of the apparatus because they were positioned upon a flake that was not continuous with the rest of the apparatus and rested at a higher level prior to removal (Fig. 1). In addition, these elements are oriented differently to the other components of the assemblage with their long processes oriented towards, rather than away from, the cusps of the M elements. They are of similar morphology, but Element 6 has undergone relatively more distortion and breakage as a result of compaction between other elements, and are interpreted here as a symmetrical pair of P elements. We discriminate the dextral and sinistral homologues of this P element position based on the consistent displacement of these elements relative to the dextral and sinistral S and M elements. Thus, Elements 5 and 6 are interpreted as dextral and sinistral, respectively. However, in contrast to the S and M elements, this pair of P elements have their denticles oriented parallel, rather than opposing, as in the S and M elements. This reflects an original difference in the orientation of the P versus S and M elements relative to the plane onto which they collapsed. Thus, there was an original large angular relationship between the orientation of these two principal suites of element positions, presumably dorso-ventral orientation of P elements relative to the largely rostro-caudal orientation of the S and M elements. Following the logic of an essentially parallel collapse orientation in ozarkodinins (Aldridge et al. 1987; Purnell and Donoghue 1997, 1998), this would require the short lateral process of these P elements to be dorsal relative to the long ventral process.

Element 4 lies with cusps and denticles opposing the surrounding S and M elements, the adaxial face is presented on the counterpart. In terms of the collapse pattern, it lies intermediate between the S (8-11) and M (1, 2) versus P (5, 6) elements. On this basis, Element 4 is interpreted as a P_2, and Elements 5 and 6 as P_1 elements. This P_2 has traditionally been described as falodontiform, and was interpreted as the M element of the *Erismodus* apparatus reconstructed by Sweet (1982, 1988). Although it has not traditionally been thought of as a P element, its morphology also lends support for this conclusion. The element is bipennate and has a flared basal sheath reminiscent of platformed P elements seen in other groups of conodonts. The opposing P_2 element to Element 4 is missing or may be represented by the denticle fragments of Group a, with the remainder of the element missing.

The remaining groups of fragmented and unidentifiable denticles (Fig. 3) are most likely to be poorly preserved parts of adjacent elements. For example, Group b lies between Elements 4 and 5 and could belong to the lateral process of either element. The denticles of Group c are consistently oriented with those of Element 6, and may represent part of that element. In contrast, the relatively robust denticles of Group d, one of which has a flared base and may be a cusp, perhaps represent another element such as the dextral S_1 or S_2 element, which are otherwise missing from the S array. Group e lies between Element 1 and Elements 8-11, and may therefore comprise the denticles of one of these elements.

Orientation of collapse

Aldridge *et al*. (1987, 1995) established that bilaterally symmetrical assemblages, such as that of *Erismodus quadridactylus*, reflect predominantly dorso-ventral collapse orientations. However, there are also elements of rostro-caudal collapse present in this assemblage and, although it is not possible to precisely constrain the vector from a single assemblage, there is evidence to suggest that the amount of rostro-caudal collapse was small. If there had been a large rostro-caudal component, then it would be expected that the elements of the apparatus would have been telescoped, with the M elements being overlain by the S elements and then these overlain by the P elements. The collapse pattern does not show this to have been the case because although the elements of the assemblage are closely spaced, they are not telescoped and the two most anterior elements actually lie discretely at the front of the apparatus.

The third component of collapse (lateral) has also affected the final pattern of the assemblage. The assemblage is slightly skewed relative to the plane of bilateral symmetry, suggesting that the apparatus collapsed somewhat laterally at an oblique angle to the substrate. The evidence for this comes from pairs of elements, Elements 1/2 and 7/10 or 11, Elements 5/6, which are offset across the midline. In addition, the sinistral half of the apparatus (Fig. 3) displays less disruption than the dextral, suggesting that this side of the animal lay directly upon the sediment during collapse. The overall preservation of the apparatus implies minimal *post mortem* disruption beyond collapse and rotation to a gravitationally stable position, with most elements preserved intact, thereby strengthening the foundation for deriving positional homologies.

COMPARISON WITH THE ARCHITECTURE OF OTHER 'COMPLEX' CONODONTS

There is a considerable body of evidence to indicate that the S and M elements of 'complex' conodonts lay rostrally within the apparatus (Aldridge *et al*. 1987; Purnell and Donoghue 1997, 1998). More specifically, the M elements lay rostro-laterally to the S array when at rest (Purnell and Donoghue 1997, 1998), whereas the P elements were oriented perpendicularly with respect to the S elements and located at the caudal end of the apparatus (Aldridge *et al*. 1987; Purnell 1993; Purnell *et al*. 1997, 1998).

The M elements in the assemblage of *Erismodus quadridactylus* lie with the long axis of their cusps almost parallel to the rostro-caudal axis of the assemblage; their outer side facing rostro-laterally; and their posterior processes adaxial whereas the 'antero-lateral' processes are abaxial. These are the same relative positions as in derived prioniodinins and ozarkodinin conodonts, and therefore it is deduced that the assemblage orientation approximates to their non-functioning *in vivo* orientation.

In ozarkodinin conodonts, the S array lies across the sagittal plane with the long axis of the cusps parallel to the dorso-ventral axis. In addition, the S elements are located successively more rostral and dorsal in an axial to abaxial direction (Purnell *et al*. 2000). The sequential layering and overlap of the S elements, in the *Erismodus* assemblage implies that they were closely spaced and also perhaps stacked with the

longitudinal axis of the cusps parallel to the dorso-ventral axis, as in the ozarkodinins. Elements 8 - 11 also show a trend whereby they become more rostral and perhaps more dorsal (although the latter dimension is not extractable from the assemblage), in a very similar way to that observed in ozarkodinin architecture.

Due to the limited data that can be extracted from this single assemblage it is not possible to deduce the precise architectural position of the P elements and their distance from other domains of the apparatus, but they do almost directly overlie the S array in the assemblage. There are two possible explanations for this. The first is that this is simply an artefact of rostro-caudal collapse (cf. Aldridge *et al.* 1987), and the second is that this position closely reflects the *in vivo* position and orientation of the P elements. With regard to the first possibility, if the apparatus collapsed in a rostrum-down orientation to the sediment then rostro-caudal telescoping of the apparatus would be expected. However, in this case the telescoping occurs only between the P and S elements and not between the M and S elements. For this reason, it is considered more likely that the P elements were closely juxtaposed to the S elements, perhaps more so than in those ozarkodinin taxa whose architecture has been described to date. This may also provide an explanation for the lack of morphological differentiation of the P, M and S domains. This proposed location of the P elements is somewhat intermediate between that in a typical ozarkodinin apparatus and that in *Promissum pulchrum*, a derived 'prioniodontid' conodont, which in comparison with ozarkodinins also has its P elements spatially closer to and dorsal with respect to the S array (Theron *et al*. 1990; Aldridge *et al*. 1995).

Although there is strong evidence for consistent apparatus composition and architectural plans in derived prioniodinin and ozarkodinin conodonts, it is by no means certain that this was also the case in more primitive prioniodinin taxa. As well as having an architecture that compares closely in some ways with ozarkodinin conodonts (specifically with four pairs of S elements located progressively more rostral and dorsal abaxially), the assemblage of *Erismodus quadridactylus* also shows evidence for similarities in topology to 'prioniodontid' apparatus architecture, particularly with regard to the position of the P elements located in close proximity to the M–S array (Figs 7-8). This supports this reconstruction of the M-S array being representative of a general ozarkodinid architecture, with more plasticity in the position (and number, see e.g. Zhang *et al.* 2017) of P elements.

INFERENCES FOR GROWTH MODELS OF PRIONIODININS

Isolated elements of *Erismodus* in collections are characterised by their very short processes (Sweet 1988). However, the assemblage data demonstrate that *Erismodus* had very long processes, a feature not preserved in discrete element collections. Coupled with data from assemblages of *Kladognathus*, which also has elements with long processes, it is highly likely that many prioniodinin conodonts possessed longer processes than is evident from discrete element data. This is a significant feature of the apparatuses of prioniodinin conodonts that needs to be accounted for in taxonomic work

and character-based analyses. Collections of isolated elements of *Erismodus* thus present a very misleading representation of the overall morphology of the elements, and are arguably relatively uninformative, or even misleading, for establishing positional homologies.

The reason for this incongruity between isolated element and natural assemblages is that the hard tissues of the processes of most elements in the apparatus are discontinuous, and are composed of discrete denticles. This is compatible with the pattern of Type 1 growth described by Donoghue (1998) in which the growth of individual denticles occurs independently.

CONCLUSIONS

The collapse pattern of the assemblage indicates that the apparatus underwent a dominantly dorso-ventral mode of collapse with lesser components of rostro-caudal and lateral collapse. The apparatus of *Erismodus quadridactylus* comprises three element domains: M, S and P. The M elements lay rostrad to the other elements of the apparatus, opposed across the midline with their cusps positioned rostrally and their posterior processes extending towards the caudal end of the animal. The S elements lie with their long axis parallel to the rostro-caudal axis. Pairs of S elements are opposed across the midline, the apices of the cusps are dorsal and posterior processes extended caudally. The P elements overlap all the other elements in the assemblage as they lie dorsal, and perhaps immediately caudal, to the S array. The apparatus architecture thus comprises aspects of both ozarkodinin and 'prioniodontid' architectures. The assemblage contains eleven complete elements; a pair of bipennate M elements, an alate S_0 element, four sinistral digyrate S elements ($S_{1\text{-}4}^{s}$), with one dextral digyrate S_3^{d} or S_4^{d} element, a pair of robust digyrate P_1 elements and a P_2 element preserved without its counterpart. When the missing S and P_2 elements, inferred from fragments in the assemblage and the assumption of bilateral symmetry, are included, the total number of elements present within the apparatus is 15.

The architecture and composition of *Erismodus quadridactylus* relative to other prioniodinins, supports conservation of the inferred prioniodinin 'blueprint' of Purnell (1993) and Purnell and von Bitter (1996). The apparatus architecture and composition of *Erismodus*, at least with respect to the M-S array, therefore reflects the general template of ozarkodinid taxa, and will help to unfold prioniodinin taxonomy. Furthermore, the more 'prioniodontid'-like position of the P elements, supports a greater degree of plasticity in the P-domain (Zhang *et al.* 2017). The presence of unfused denticles in the long processes of all digyrate elements in the apparatus also highlights the caution with which isolated elements can be used to establish positional homologies, particularly if discrete denticles are recovered from the same sample horizons.

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DATA ARCHIVING STATEMENT

Tomographic data and supporting information are available at the Bristol Research Data Repository. https://data.bris.ac.uk/webshare/glpcjd-donoghue-2012/9e4fe100-8867-4b99-89c8-428653ed951f/

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FIGURE CAPTIONS

FIGURE 1. Scanning electron micrograph of an assemblage of *Erismodus quadridactylus* (Stauffer, 1935), USNM 542388, part. A, complete specimen, imaged in secondary electron mode; B, following preparation and removal of a loose flake in order to search for additional elements, imaged in back-scatter mode. The assemblage is from Sandbian (Late Ordovician) strata in the Shell Oil Duerre 43-5 well, which was drilled in section 5, Township 163 North, Range 87 West, in Renville County, North Dakota, USA. The well is in the Newporte Field of the Williston basin. The specimen is deposited in the National Museum of Natural History, Washington DC, USA. Scale bars, 1 mm.

FIGURE 2. Scanning electron micrograph of the assemblage of *Erismodus quadridactylus* (USNM 542388), counterpart. A, imaged in secondary electron mode; B, imaged in back-scatter mode. Scale bars, 1 mm.

FIGURE 3. Composite line drawing of the part and counterpart of the assemblage of *Erismodus quadridactylus*. For clarity, the sinistral elements are shown in mid-grey and the dextral elements are shaded in dark grey. Mouldic elements are outlined by dashed lines and those elements not assigned to any numbered element are shaded in white and outlined with a solid black line. The element numbers correspond to those used in the text. Element 3 is symmetrical and unpaired. Element 4 cannot be confidently assigned as dextral or sinistral, and for this reason is shaded white. The evidence indicates that the apparatus underwent dominantly dorso-ventral collapse with minor components of rostro-caudal and lateral collapse, although it is not possible to precisely constrain these vectors due to the availability of only a single assemblage.

FIGURE 4. Reconstruction of *Erismodus quadridactylus* (Stauffer, 1935), USNM 542388, based on CT data. Shown viewed as in the part (Fig. 1) and the counterpart (Fig. 2). The rostro-caudal axis is approximately horizontal on the page in both (A) and (B); in (A) rostral is to the left, and in (B) rostral is to the right. Volume renderings are of preserved apatite both on and below the surface of the slab, therefore some elements are incomplete, where parts of the elements are preserved only as mouldic impressions. Element numbers refer to those in the text and in Figs 3 and 8.

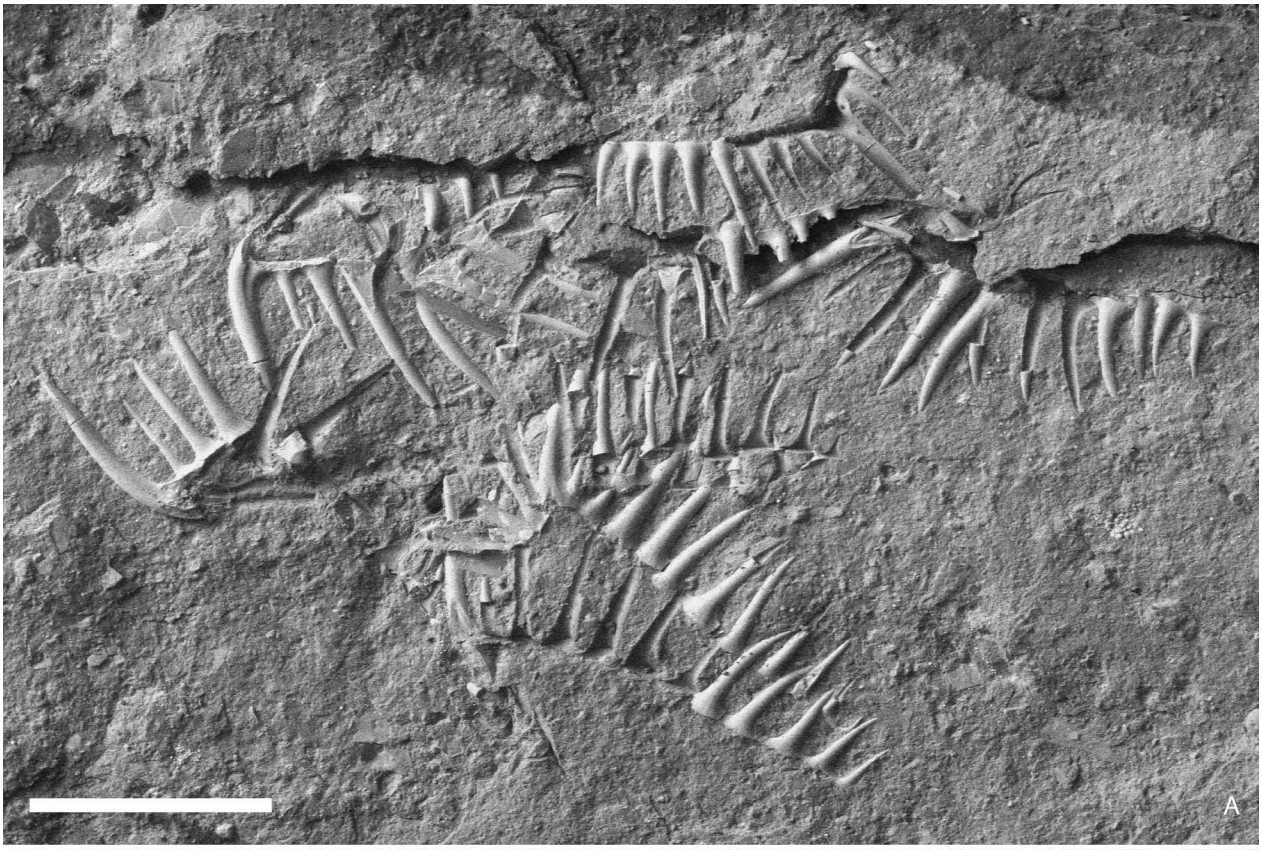
FIGURE 5. Reconstruction of elements of *Erismodus quadridactylus* (Stauffer, 1935), USNM 542388, based on CT data. Shown viewed as in the part (Fig. 1) and counterpart (Fig. 2). Volume renderings are of preserved apatite both on and below the surface of the slab, therefore some elements are incomplete, where parts of the elements are preserved only as mouldic impressions. In the case of element 6, it is almost entirely preserved as a mouldic impression, and consequently not shown here. Element numbers

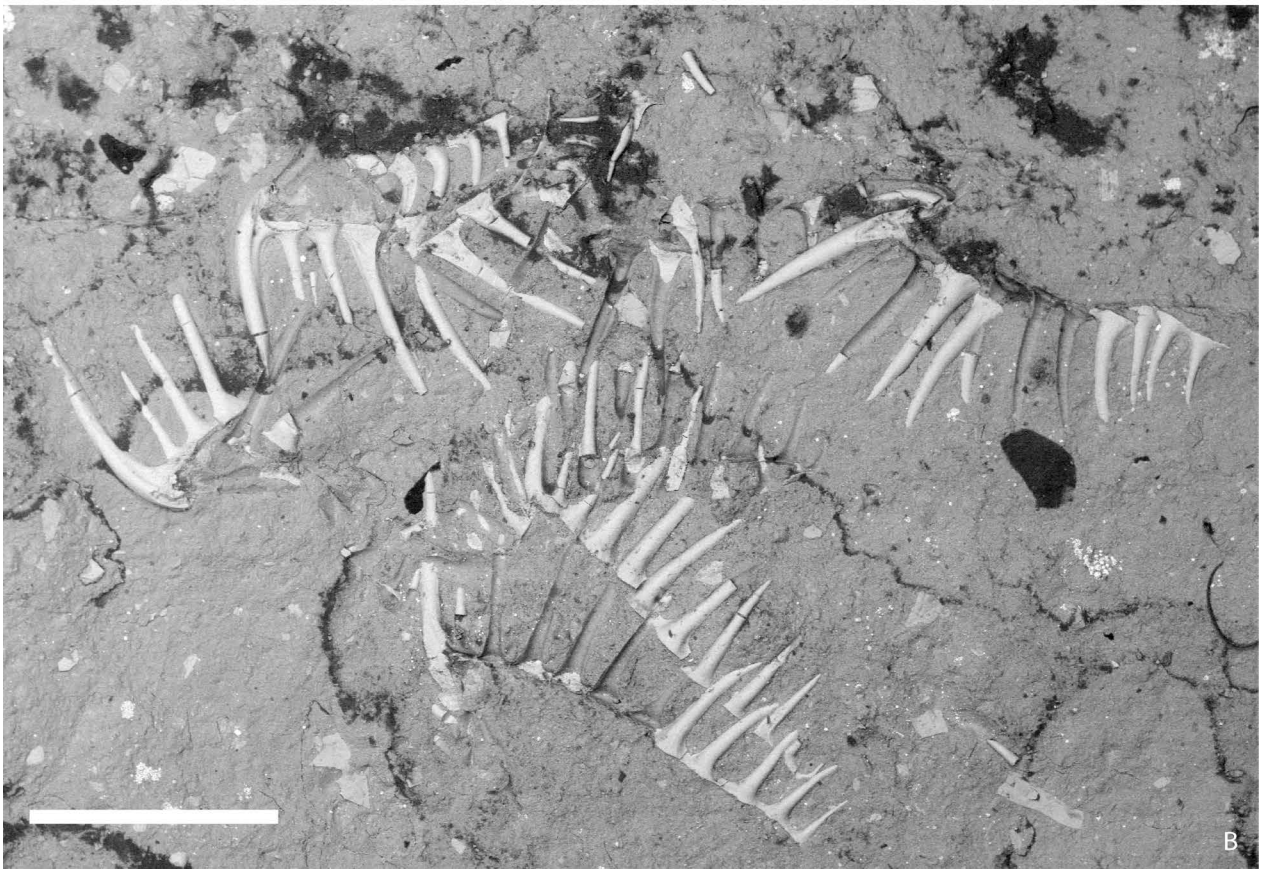
and homologies refer to those in the text. Nomenclature of Purnell *et al.* (2000); superscript ‘s’ indicates sinistral elements, and ‘d’ denotes dextral elements.

FIGURE 6. Apparatus reconstructions of *Erismodus quadridactylus* based on isolated element collections from Sweet (1982), Hall (1986) and Bauer (1990) compared with that based on the assemblage from North Dakota and a collection of isolated elements from the Harding Sandstone of Colorado, USA. The upper panel shows the schematic element morphology and notation based on the assemblage; lateral process orientations are indicated and the white arrows illustrate cusp orientation. The middle panel illustrates the element morpohology and notation used by Sweet (1982); note that several elements have moved position, and domain, based upon the constraints provided by the assemblage. The lower panel depicts the elements from previous reconstructions of *Erismodus* alongside the elements of the assemblage and material from the Late Ordovician Harding Sandstone of Cañon City, Colorado.

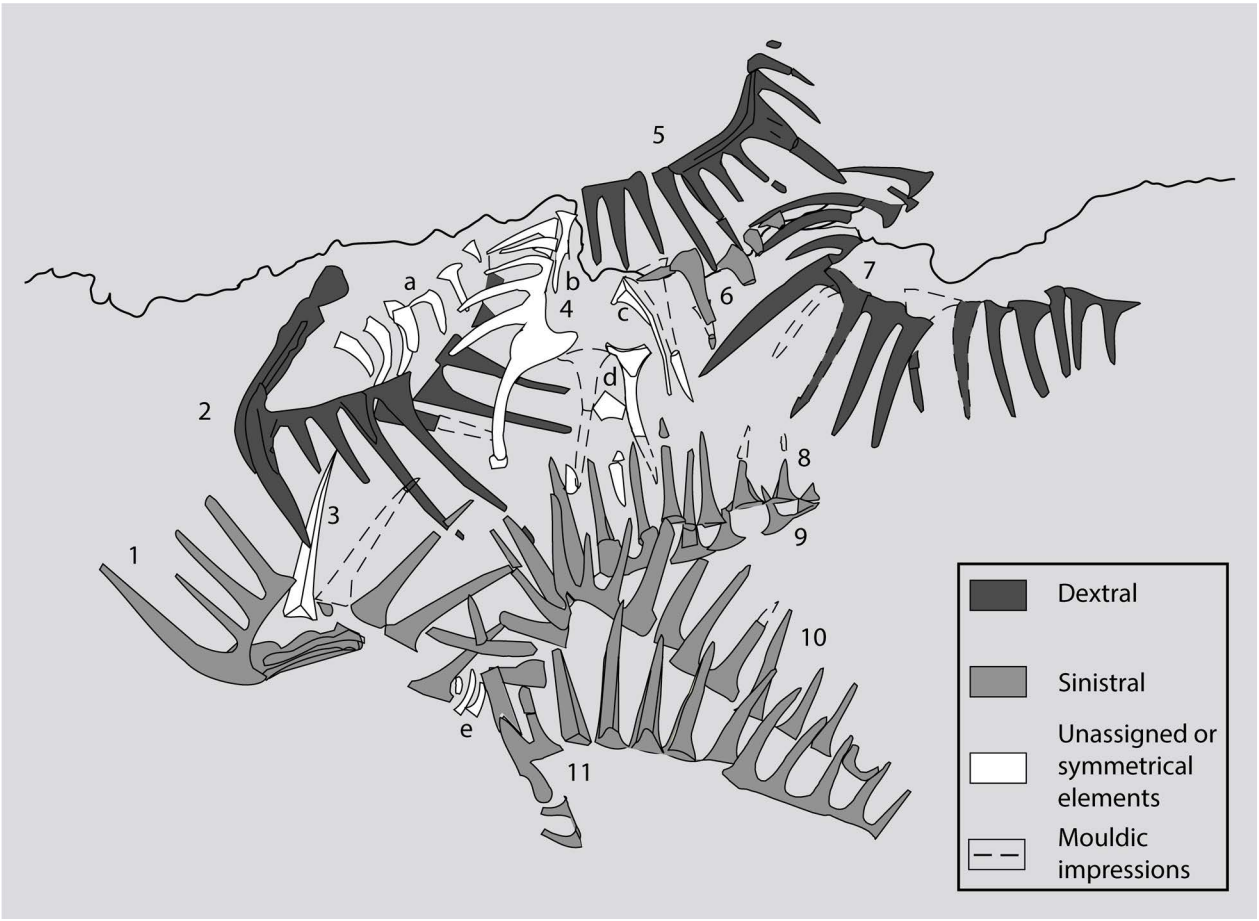
FIGURE 7. Schematic maps of relative element positions and topological notation. A, typical ozarkodinin architecture (after Purnell *et al*. 2000); B, the apparatus architecture of *Erismodus* based upon the North Dakota assemblage. Lateral process orientations are indicated and the white arrows illustrate cusp orientation. Element numbers used in Fig. 3 and the text are indicated next to each element and the possible affinities of unidentified denticle groups are also shown.

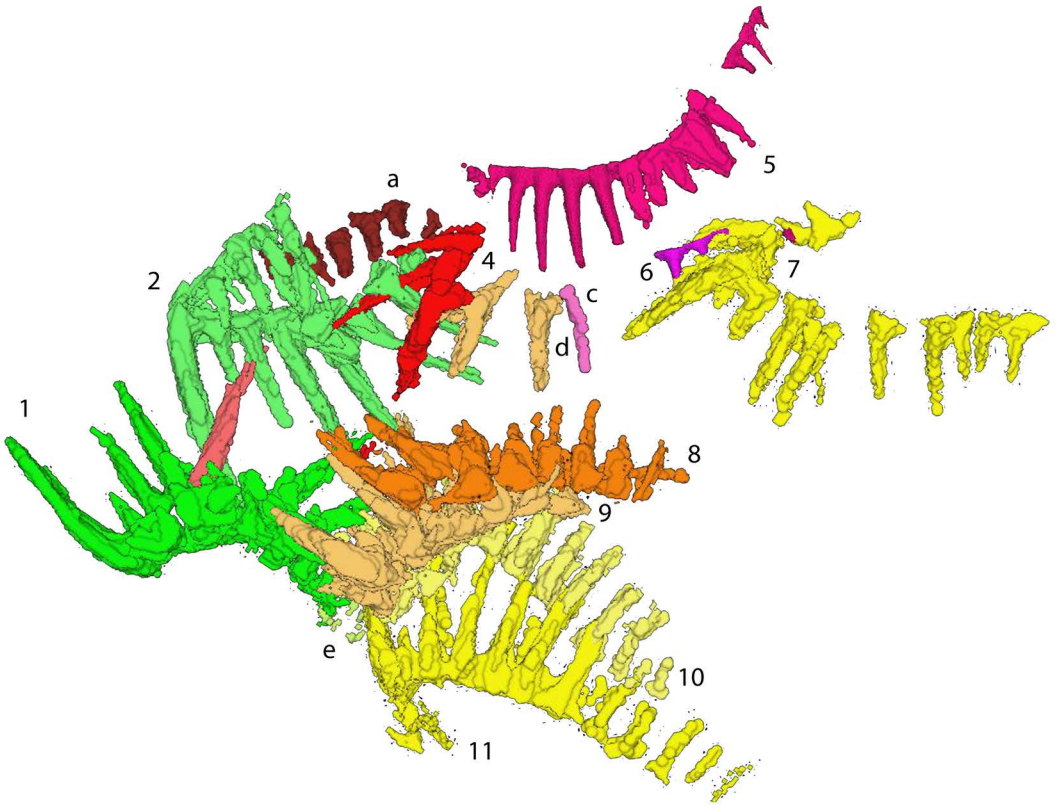
FIGURE 8. Composite line drawing of the part and counterpart of the assemblage of *Erismodus quadridactylus* with elements coloured according to architectural domain. Element fragments that have not been definitely assigned remain shaded in white. The solid black line in the upper section of the figure outlines a loose flake of sediment, which has since been removed (compare Figs 1B and 2B). Superscript ‘s’ indicates sinistral elements, and ‘d’ denotes dextral elements.


A

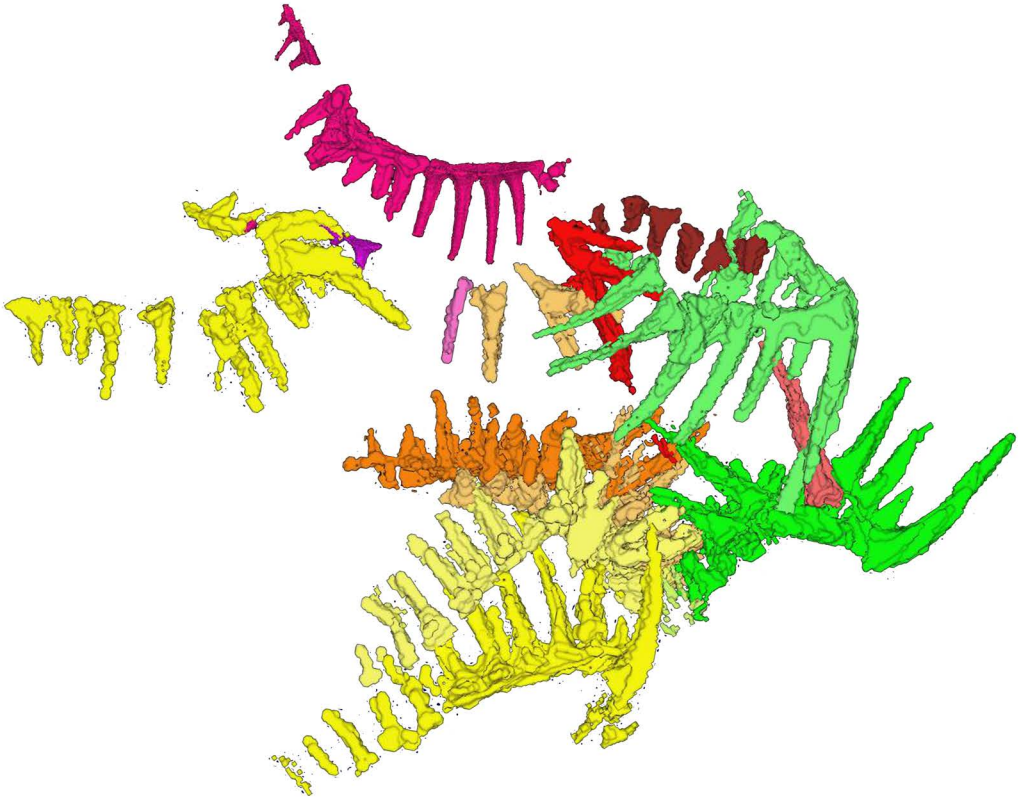

B


A
B

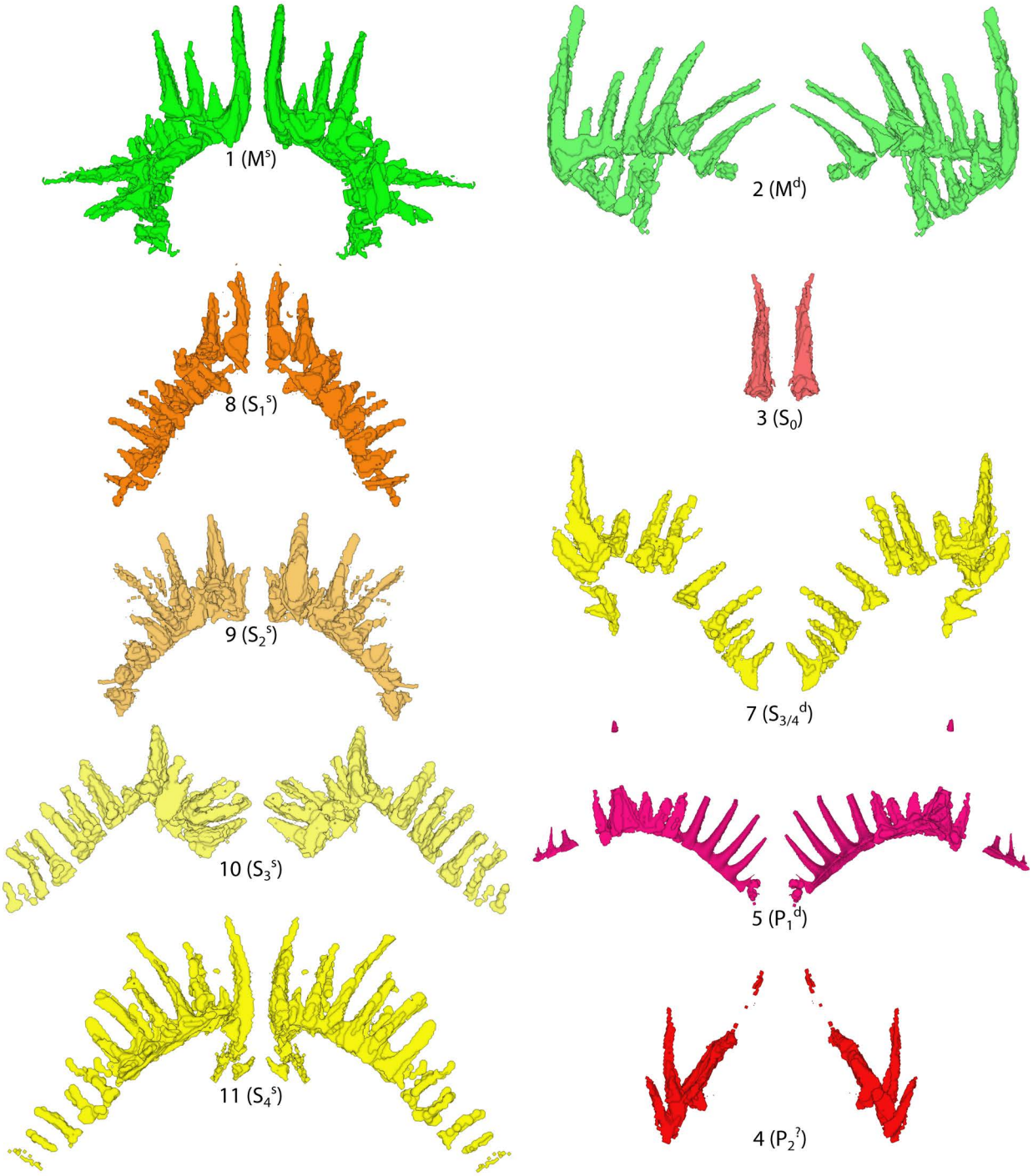

5
a
b
4
c
6
7
d
2
8
3
1
9
10
e
11
Dextral
Sinistral
Unassigned or symmetrical elements
Mouldic impressions

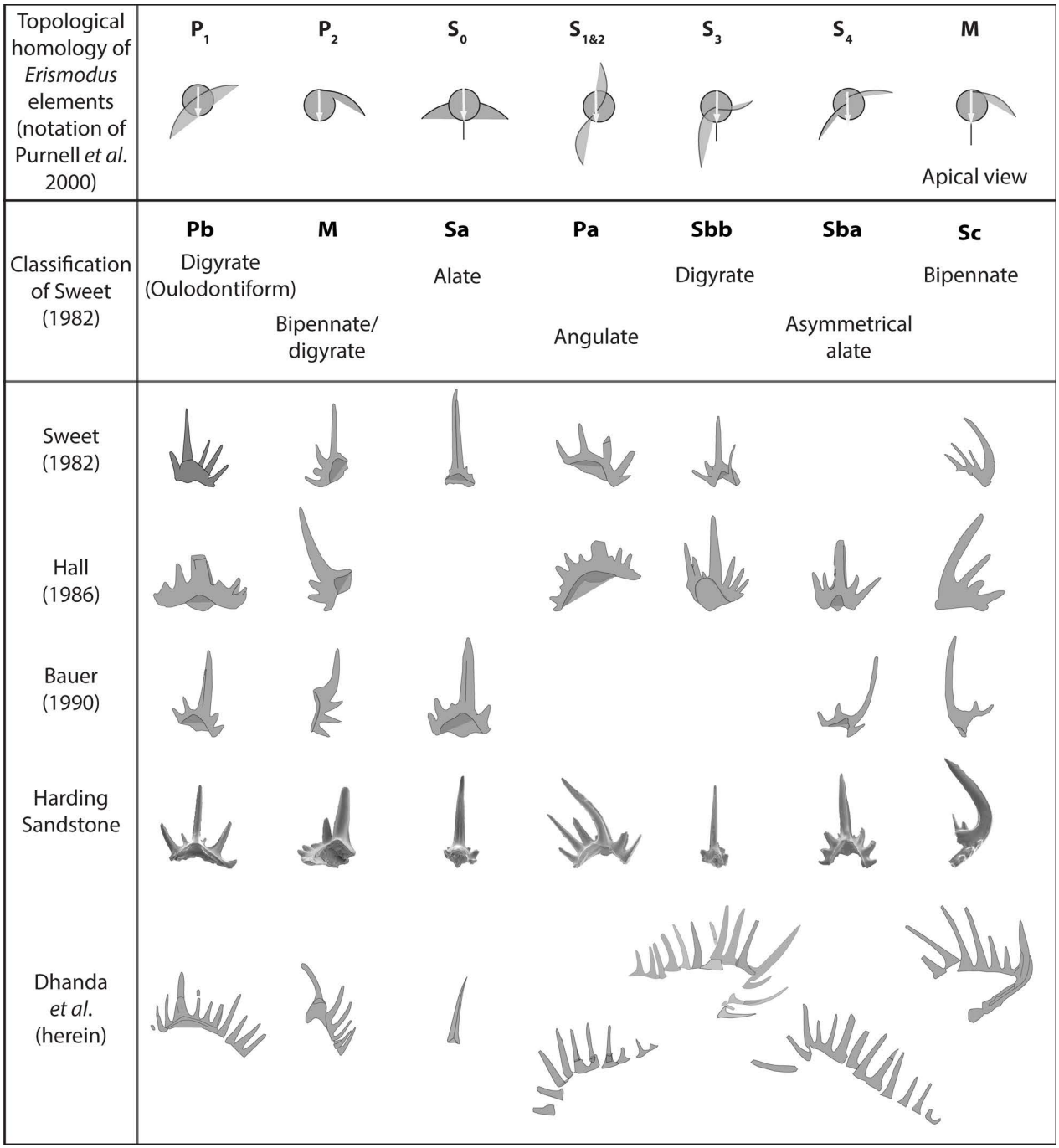


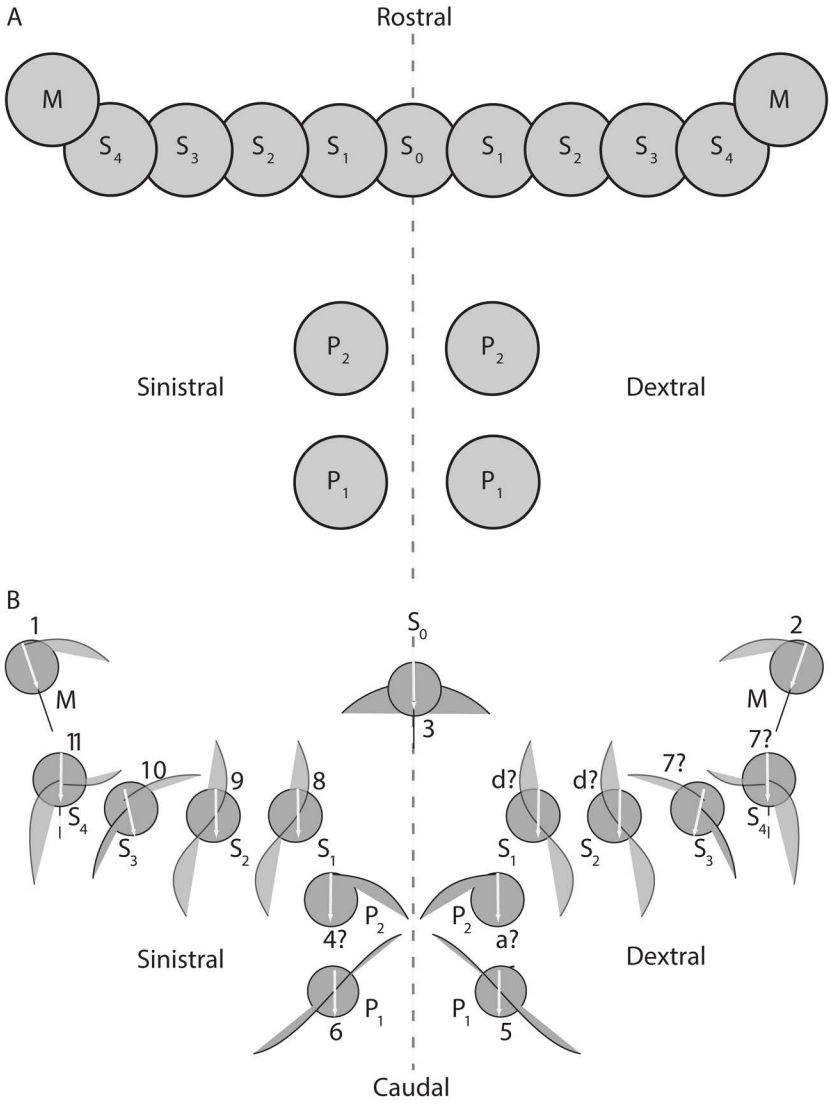
A

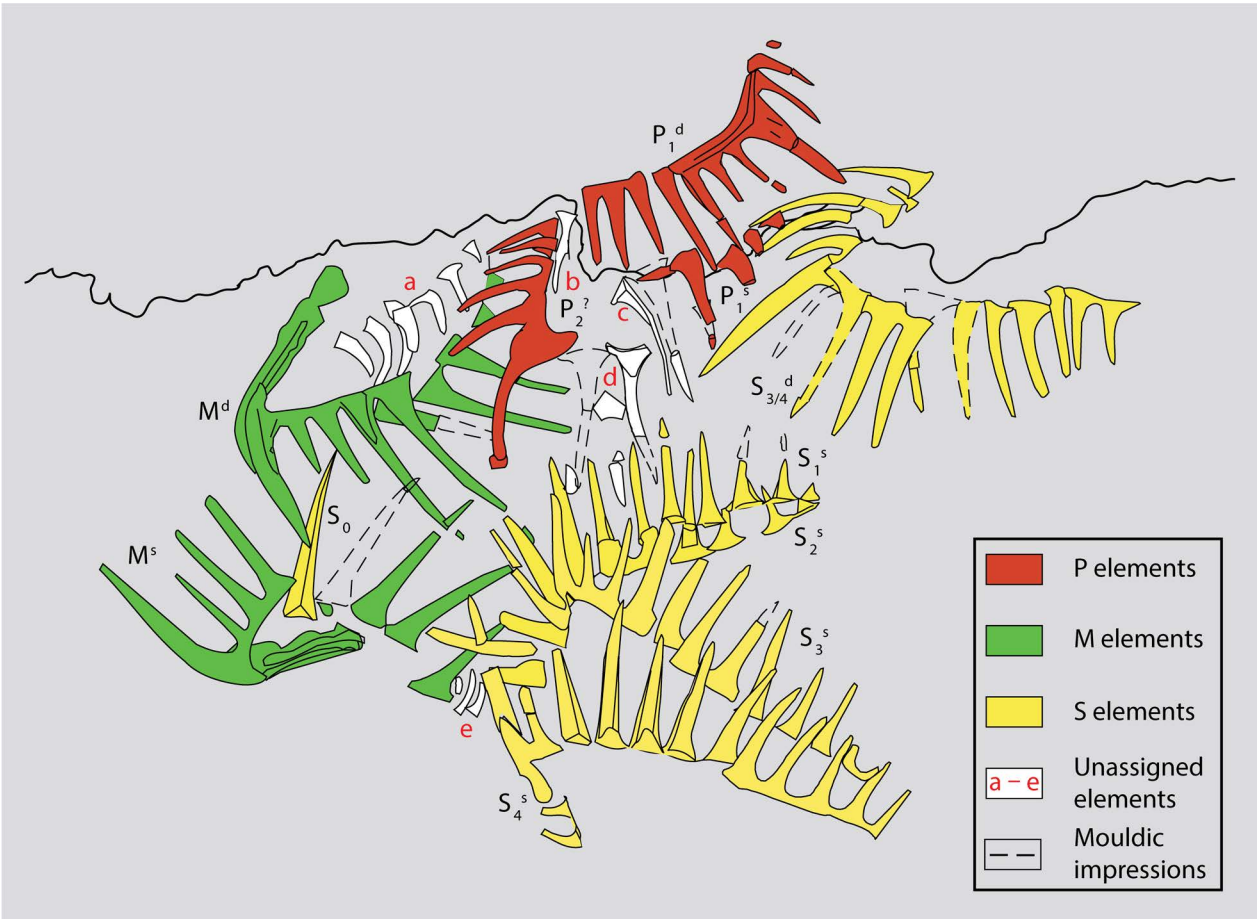


B


1 (M^s)
2 (M^d)
8 (S1^s)
3 (S0)
9 (S2^s)
7 (S3/4^d)
10 (S3^s)
5 (P1^d)
11 (S4^s)
4 (P2^?)


Topological homology of *Erismodus* elements (notation of Purnell *et al.* 2000)
P1
P2
S0
S1&2
S3
S4
M
Apical view
Classification of Sweet (1982)
Pb
Digyrate (Oulodontiform)
M
Bipennate/ digyrate
Sa
Alate
Pa
Angulate
Sbb
Digyrate
Sba
Asymmetrical alate
Sc
Bipennate
Sweet (1982)
Hall (1986)
Bauer (1990)
Harding Sandstone
Dhanda *et al.* (herein)


A
Rostral
M
S4
S3
S2
S1
S0
S1
S2
S3
S4
M
P2
P2
Sinistral
Dextral
P1
P1
B
1
M
11
S4
10
S3
9
S2
8
S1
S0
3
2
M
7?
S4
7?
S3
d?
S1
d?
S2
P2
4?
P2
a?
P1
6
P1
5
Sinistral
Dextral
Caudal


P 1 d
a
b
P 2 ?
c
P 1 s
d
S 3/4 d
M d
S 1 s
S 0
S 2 s
M s
S 3 s
e
S 4 s
P elements
M elements
S elements
a – e
Unassigned elements
Mouldic impressions